

INTERSPECIFIC HYBRIDISATION IN THE COCCINELLIDS: SOME OBSERVATIONS ON AN OLD CONTROVERSY

By HEATHER IRELAND, PETER KEARNS and MICHAEL MAJERUS*

Suggestions by Marriner that *Adalia bipunctata* Linn. and *Adalia decempunctata* Linn. freely interbreed to produce the hybrid *biabilis* Marriner, have been justifiably refuted by Capra. Here we report the production of hybrids between these two species. We show that the hybrids are extremely variable in colour and pattern; that they are generally sterile; and that examination of the genitalia indicates diagnostic features by which the hybrids may be identified.

Reports of interspecific hybridisations in ladybirds are rare, but Marriner (1926) published some sparse notes on hybridisation experiments between the two-spot ladybird (*A. bipunctata*) and the ten-spot (*A. decempunctata*). His experiments started with the chance observation of a hybrid mating between these species in one of his breeding boxes. He did not give the number of crosses he carried out, or the number of progeny he obtained, but he found an unusual form in the offspring. This he called *Coccinella* hyb. *biabilis*, and despite the fact that he knew individuals of this type were found in the wild, he argued that it was a true hybrid. In fact, he thought it occurred in natural populations as the result of wild hybridisations. He even speculated that the wild hybrids might be "a new species in process of evolution".

The conclusions of these experiments were convincingly rejected by Capra (1926). He pointed out that *biabilis* figured by Marriner is not exceptional as it is a recognised form of *A. decempunctata*, that is to say, f. *decempustulata* Linn. (see Mader, 1926-1937) which is common throughout Europe, and is in fact, one of the forms described by Linnaeus. In addition, he criticised Marriner for not describing the conditions of his experiments, and for the lack of detail on the precautions taken to isolate mating pairs and their offspring. He suggested that Marriner had observed a hybrid mating, and together with the presumed offspring of this pair, reared other specimens of both species from his mating cage; but only when he observed the postulated hybrid offspring, did he think of its origins. Capra said that it was more likely that the hybrid was simply a form of *A. decempunctata*. This seems plausible as f. *decempustulata* is said to be genetically recessive to the nominate form, *decempunctata*, so it is quite reasonable that this form should segregate out from a parental population in which it is absent. Capra's conclusions are further justified when one considers the vague description of the

*Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH.

experiments, which was given by Marriner. As a result, Marriner's conclusions have been largely discounted (see Iablokoff-Khnzorian, 1982).

We have doubts about some of Marriner's other general observations in his 1926 paper. For example, he suggested that typical forms of *A. bipunctata* predominate in the spring, while melanic forms predominate later on in the summer months. This is not the case in British populations (Creed, 1966, 1975; Muggleton, 1978; Majerus, pers. obs). Some of his data appears nonsensical for he reports an increase in the frequency of melanic forms from 30% to 82% in an unspecified locality between June 1921 and August of the same year, and reports that these figures were repeated in several other years. The selective coefficients to produce this change are extremely improbable. We also disagree with his observation that typical forms of *A. bipunctata* are more difficult to rear than the melanic forms. We have reared thousands of specimens of both forms and find no obvious differences in fertility, viability or fecundity; and when all our data is pooled from broods in which both melanic and typical forms segregate, it is the *typica* form which is in excess over expectation. He also states that under starvation conditions, dark forms do not die off as quickly as typical forms; again we disagree and suggest that the reverse is in fact true.

Although we are convinced by Capra's arguments, we decided to attempt to hybridise *A. bipunctata* and *A. decempunctata*, because the debate could never be properly resolved until critical experiments were carried out. Probably the most important requirement was to begin by obtaining individuals of both species which we knew to be virgin. So we isolated a number of ladybirds of each species as soon as they emerged from their pupae, and kept each individually for about a fortnight before they were used for crosses.

Six pairs were set up initially, each couple being kept isolated in a petri-dish. They were fed every day on live pea aphids (*Acyrtosiphon pisum* Harris), which were added to the petri-dishes. The two species readily mated, but the vast majority of the eggs which were laid were infertile. However, two crosses produced a few fertile eggs and these eventually led to adult hybrids. One cross was between *A. bipunctata* f. *pruni* Ws., and *A. decempunctata* f. *decempustulata*. This cross produced 10 progeny. The second cross was between a melanic *A. decempunctata* f. *bimaculata* Pont., and a melanic *A. bipunctata* f. *quadrimaculata* Scop. This produced just two progeny. The parents and some of the progeny of these two crosses are shown in figures 1a and 1b.

Various investigations were carried out on the adult hybrids. Firstly, the patterns on the elytra show that they are not of a single hybrid type as inferred by Marriner, but rather, they display a great variety of patterns. So from the first cross, some progeny had elytra which were more or less like the *A. bipunctata* parent.

The pronota of these were *bipunctata*-like in one, and *decempunctata*-like in the others. Other progeny were similar to the *A. decempunctata* parent, but had *bipunctata*-like pronota. Still others were similar to the more normal types of *A. decempunctata*, so fig. 1a shows one offspring which is indistinguishable from *f. octomaculata* Mull. It is notable that all the progeny had brown or orange legs, characteristic of *A. decempunctata* (in Britain *A. bipunctata* has black legs). The two offspring from the second cross were most curious as both were almost completely black, and so unlike either parent. Again, they had brown rather than black legs.

Secondly, the hybrids were tested for fertility, but they were found to be infertile both in crosses amongst themselves and with either true *A. bipunctata* or *A. decempunctata* mates. Dr. S. A. Henderson (Department of Genetics, Cambridge) examined four males and found a variety of causes to account for their sterility. In one case, the testes were malformed and in another, there appeared to be no sperm formation. Finally, in two cases, the chromosomes behaved aberrantly during sperm formation so that chromosome breakages, and univalent chromosomes, were common.

Finally, the hybrids were examined by Mr. R. D. Pope (British Museum, Natural History). His opinion is that while the hybrids have unique features, they also share characteristics with both parent species. For example, all the hybrids have the strong look of *A. decempunctata*, but with the black mesapimera and metapimera of *A. bipunctata*. His other major observation was that the infundibula of all the female hybrids were similar to each other, and they were unique, being readily distinguished from those of both parental species. Despite this, the female genitalia had more in common with *A. bipunctata* than *A. decempunctata*.

We have subsequently obtained three progeny from another hybrid cross between *A. decempunctata* f. *decempustulata* and *A. bipunctata* f. *bipunctata* (see fig. 1c). In this case, all the progeny were fairly similar to *A. bipunctata*, but again had brown legs.

Although we cannot be certain, the results of our work lead us to the conclusion that Capra was right in claiming that Marriner did not obtain genuine hybrids; despite the fact that the two species do hybridise. If Marriner had obtained genuine hybrids it is unlikely that he would have obtained only the form *biabilis/decempustulata*.

Despite the probability that Marriner did not obtain hybrids, our final observations are concerned with his suggestion that the hybrid between *A. bipunctata* and *A. decempunctata* might be a new evolving species. This seems unlikely because hybrid matings are rare in the wild though they have been occasionally observed. Furthermore, although we have obtained hybrid matings in the laboratory, fewer than 1% of any eggs laid are viable.



Figure 1a. Hybrid cross 1. *A. decempunctata* f. *decempustulata* parent (top left) x *A. bipunctata* f. *pruni* parent (top centre), with five hybrid progeny.

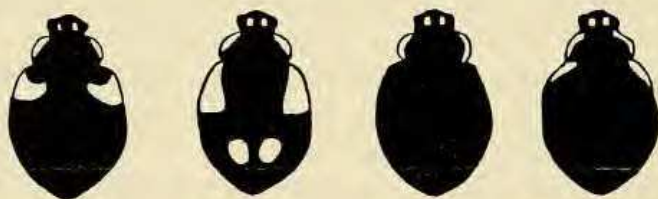


Figure 1b. Hybrid cross 2. *A. decempunctata* f. *bimaculata* parent (extreme left) x *A. bipunctata* f. *quadrinaculata* parent (inside left), with hybrid progeny.

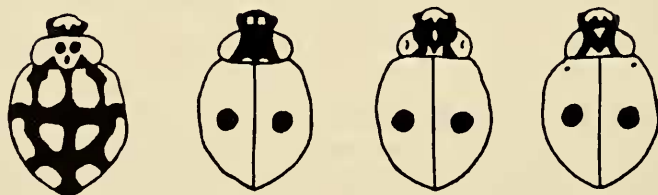


Figure 1c. Hybrid cross 3. *A. decempunctata* f. *decempustulata* parent (extreme left) x *A. bipunctata* f. *bipunctata* parent (inside left), with hybrid progeny.

In fact, the process of speciation by interspecific hybridisation seems to have been at best, very rare in the animal kingdom, because of the infertility of hybrids. This normally occurs because of differences between the two sets of parental chromosomes, which means they are unable to pair and separate correctly during gamete formation. Speciation through interspecific hybridisation is known among plants, because they are more readily able to indulge in polyploidy. This occurs when the chromosomes replicate without subsequent cell division, thus producing cells which contain two copies of each chromosome. These can then pair and divide normally. In animals polyploidy is extremely rare. In any case, the fact that the ladybird hybrids are sterile as the result of malformations in both gonads and chromosome structure, means that the two species are reproductively isolated from each other. This is entirely consistent with the normal pattern of interspecific hybridisations in animals, so it is extremely unlikely that Marriner's suggestion is true.

Acknowledgements

We thank Dr. S. A. Henderson and Mr. S. Albrecht for their cytological studies and Mr. R. D. Pope for his morphological and anatomical investigations. We would also like to thank Ms. D. Sommaro for her translation of Capra's original paper.

References

- Capra, F. (1926) Su un preteso ibrido tra Coccinellidi. *Coccinella* *hyb. biabilis* Marriner. *Boll. Soc. Ent. Ital.* **58**: 113-116.
- Creed, E. R. (1966) Geographic variation in the two-spot ladybird in England and Wales. *Heredity* **21**: 57-72.
- Creed, E. R. (1975) Melanism in the two-spot ladybird. The nature and intensity of selection. *Proc. R. Soc. B.* **90**: 135-148.
- Iablokoff-Khnzorian, S. M. (1982) *Les Coccinelles*. Boubee, Paris.
- Mader, L. (1926-1937) Evidenz der palaarktischen Coccinelliden und ihrer Aberrationen, In Wort und Bild, I. *Epilachnini, Coccinellini, Halysiini, Synonychini*, XII + 412, 64 T., 15 fig. (1926-1934, Wien, Verein Naturbeobachter und Samml., 1935, *Ent. Anzeig.*, **15**: 329-383, 1937, *Ent. Nachr. Bl.*: 384-412).
- Marriner, T. F. (1926) A Hybrid Coccinellid. *Ent. Rec.* **38**, 81-83.
- Muggleton, J. (1978) Selection against the melanic morphs of *Adalia bipunctata* (Two-spot ladybird): a review and some new data. *Heredity* **40**, 269-280.